A MONOGRAPH OF THE GENUS PROSOPIS (LEGUMINOSAE SUBFAM. MIMOSOIDEAE)

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THIS MONOGRAPH of *Prosopis* is the result of prolonged herbarium and field studies made over a period of several years with the intention of completing an exhaustive treatment of an important but difficult genus. The monograph represents the completion on a world scale and a revision of my earlier paper "Materiales para una monografía del género *Prosopis* (Leguminosae)" (Darwiniana 4: 57–128. 1940), which found wide acceptance for its more natural definition of the species. For the Mexican-Texan area of the genus, the work by M. C. Johnston (Brittonia 14: 72–90. 1962) on sect. ALGAROBIA was very helpful. Encouragement to write this paper came from those botanists interested in a broad research project on *Prosopis* (Structure of Ecosystems Program of the US/IBP).

I am conscious that this is not a final treatment and that amendments may be necessary as the results of new research become available. However, workers in nontraditional fields of phytotaxonomy and biology need up-to-date systematic accounts of the plants which they study.

My visits to the principal botanical institutions of the United States in 1973 and 1975, after I had seen most Argentine herbaria, gave me the final opportunity to finish this paper. I have to acknowledge with gratitude the interest and help received from many colleagues and friends during this task. Professor Otto Solbrig (Gray Herbarium, Harvard University, Cambridge, Massachusetts), Dr. Beryl Simpson (U. S. National Herbarium, Smithsonian Institution, Washington, D. C.), Dr. Marshall C. Johnston (University of Texas, Austin), and Dr. Peter Raven (Missouri Botanical Garden, St. Louis, Missouri) have to be mentioned in this connection. My thanks are also extended to the staff of the journal of the Arnold Arboretum for valuable editorial work.

* Professor Arturo Burkart, whose extensive treatment of *Prosopis* we are publishing here, visited the Harvard University Herbaria in the spring of 1975. I had previously reviewed the paper in some detail and was able to discuss various matters of arrangement and style with him. He seemed happy that publication would be possible within a year and gave me permission to make any changes in the English that I thought were necessary. Aside from normal editorial alterations, I have made changes only where not to have done so would have left the meaning obscure.

Professor Burkart died only a few weeks after leaving Harvard. We are glad to be able to publish this paper, which embodies some of his great knowledge of and experience with the Leguminosae, a plant family he studied all his life and which he knew better than almost anyone else in the New World.

Arturo Burkart was a helpful colleague and a good friend for many years. His passing is a great loss to American botany. We hope he would have been pleased with this publication of his study of *Prosopis*, his favorite genus. B. G. Schubert.

GENERIC DIAGNOSIS

Prosopis Linnaeus emend. Burkart.

TYPE SPECIES: *Prosopis spicigera* Linnaeus, Mantissa Pl. 68. 1767; cf. A. Burkart, Darwiniana 4: 59, 61. 1940. Now a synonym of *P. cineraria* (L.) Druce.

Flowers small, actinomorphic, pentamerous, hermaphroditic; aestivation valvate; calyx campanulate; corolla with linear petals, these fused or more or less free, glabrous or pubescent, frequently villous or pilose inside toward the tip; androecium of 5 + 5 free stamens; anthers elliptic, dorsifixed, introrse, with an apical, pedicellate, globose or ovoid connectival gland; pollen grains simple, isopolar, tricolporate, subspheroidal to prolate, the exine pertectate, baculate, the sexine bigger than the nexine, the grains large or small; ovary stipitate, villous or sometimes glabrous. Anthesis apparently protogynous, the filiform style emerging from the flower bud before the stamens appear; flowers greenish-white, yellowish with age, seldom red; insect-pollinated.

Fruit a modified indehiscent legume called a drupaceous loment, linear, straight, falcate, annular to spirally coiled; mesocarp fleshy, sugary or fibrous; endocarp divided into 1-seeded, coriaceous to bony segments, closed or sometimes opening easily, longitudinal or rarely biseriate and transverse; seeds ovoid, compressed, with fissural line on the faces (pleurogram), hard, brown, with mucilaginous endosperm (typical of Mimosoideae) surrounding the embryo; cotyledons flat, rounded, epigeous in germination.

Trees or shrubs of varying size, rarely subshrubs, predominantly xerophilous, aculeate, spiny or rarely unarmed. Leaves bipinnate, commonly with few pairs of opposite pinnae, only in a few subaphyllous species sometimes reduced, pinnate, paucifoliolate; petiole with circular, sessile, apical gland and sometimes smaller, similar ones on the rachis of the pinnae; leaflets small, numerous, mostly opposite, linear, oblong, fusiform, rarely large (*P. ruscifolia*), entire, of the same color on both sides; venation pinnate, not very prominent.

Racemes spikelike, amentiform, axillary, mostly densiflorous, sometimes with globose heads.

Shoots in most species dimorphic; megablasts long, flexuous, knotty in age; brachyblasts or short shoots emerging from multiple axillary buds (which develop the cauline spines when extant), leaf fascicles, and racemes.

CHROMOSOMES. The *Prosopis* species are mainly, if not entirely, diploid, with the somatic number of $2n = 28$. Polysomaty in root tips (cortical cells) is frequent and probably responsible for false tetraploidy interpretations, e.g., in *P. juliflora*. A supposedly tetraploid species from the Pacific Islands, *P. insularum* (Guill.) Breteler does not belong to the genus, but to *Schleinitzia* Warburg. Chromosomes in *Prosopis* are small

and uniform, without special distinctive marks. Meiosis seems to be normal even in supposedly hybrid populations.

DISTRIBUTION. About forty-four species distributed in Southwest Asia, Africa, and predominantly America, from western North America to Patagonia, mainly in warm and dry regions of the West, with the center of polymorphism in Argentina. Some species are cultivated and naturalized outside their original homes.

ECOLOGICAL AND ECONOMIC IMPORTANCE. Because of their abundance and ecological behavior, the *Prosopis* species are important vegetation elements in arid and semiarid countries, where many of them offer shade, firewood, timber, and food for man and shade and forage for wildlife and domestic herbivores. Their importance for Indian cultures has been very great in the past and is still considerable, in spite of much devastation. Not to be neglected is the value of the flowers as bee pasture. The edible fruits of some species and varieties are used as food in the form of meal or fermented beverages; however, these products have not yet gained general acceptance.

Some species, especially the mesquite (*P. glandulosa*) in Texas and the vinal (*P. ruscifolia*) in the Chaco, because of their tremendous invading power, have become nuisances to ranchers and are fought with all kinds of herbicides. Other species are planted for shade and forage in the tropics.

Ecologically, the legumes are important for the endozoic propagation of the hard seeds, which germinate freely after passing through the digestive tracts of cattle, sheep, goats, or wild animals such as the guanaco, the South American ostrich, the fox, etc. According to information given to me by O. T. Solbrig, not only are the fruits, if eaten, dispersed by the animals, but their passage through the digestive tract also benefits the seed by killing the Bruchid beetles (specialized legume predators) always present in *Prosopis* fruits. The nutritive legumes, with seeds resistant to the digestive juices of herbivores, demonstrate a superior adaptation of the species of *Prosopis* in their struggle for survival and dispersal.

There is a real need for more ecological studies on these species and for a selection program to aid forestation plans in arid and semiarid regions. Superior strains, especially of such useful species as *P. juliflora, P. chilensis, P. pallida, P. caldenia, P. alba, P. nigra, P. affinis, P. tamarugo,* etc. should be cultivated and tested at experiment stations of dry-climate countries in order to have them ready for large forestation programs.

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GENERIC LIMITS AND SUBDIVISIONS

Because of the uniformity of leaf, floral, and fruiting characters, there seems to be no reason for a subdivision of the genus such as was proposed by Britton and Rose (North American Flora **23**: 180, 182–187. 1928) and followed in part by Hutchinson (1964).

The paribipinnate leaf, characteristic of the whole subfamily Mimosoideae, presents in most species of *Prosopis* only one or a few pairs of pinnae and never a solitary apical pinna, found, for instance, in the leaves

of *Caesalpinia* and *Hoffmanseggia* and other caesalpinioid genera, but entirely absent in the Mimosoideae.

Flowers in *Prosopis* are of the common actinomorphic, pentamerous, decandrous, hermaphroditic type, with gland-tipped anthers, apparently the primitive model of a mimosoid floret.

The fruit, a modified, indehiscent, more or less fleshy legume with the endocarp commonly hardened and segmented into one-seeded joints, is of a type which I have called "*lomento drupáceo*" (*lomentum drupaceum*; Burkart, Las Leguminosas Argentinas, sylvestres y cultivadas 21. 1943; *Ibid.* ed. 2. 17. 1952). In spite of the diversity of forms and curling, the fruit is fundamentally uniform, another sound reason for maintaining *Prosopis* sensu lato, essentially as it was established by G. Bentham. Too much weight has been given to the curvature and curling of the *Prosopis* fruit and its bearing on systematics. There is a parallel development in both main sections (STROMBOCARPA and ALGAROBIA), with variation from nearly straight to curved and spirally coiled loments. Only one difference exists; the closed corkscrew type is reached by only some members of sect. STROMBOCARPA, while in sect. ALGAROBIA the spirals are always fewer, larger, and open. This difference is of importance at the specific level.

In contrast with this uniformity of the fruit, there is a marked vegetative diversification in the armature, whether it consists of spines or prickles or is absent. These differences provide the best foundations for a sectional subdivision of the genus. Most authors of local treatments of *Prosopis* fail to recognize the importance of these differences of subgeneric rank, although I devoted a special paper to them (Burkart, 1937). Britton and Rose, for example (*loc. cit.*), made no distinction between "stipular spines" or "spinescent stipules" in their "genera" *Sopropis*, *Strombocarpa*, and *Neltuma*. Relying on the differences of armature to provide the only strict differences between sections, we may trace the following scheme, which notwithstanding its morphological nature possibly has phylogenetic significance:

1. Primarily unarmed. African species. ..... Sect. ANONYCHIUM (species 4).
2. With cauline prickles (internodal hard emergences like the aculei of *Rosa* and *Rubus*). Asiatic and North African species. ..... Sect. PROSOPIS (formerly sect. *Adenopis*) (species 1–3).
3. With stipular (foliar) spines; stipules very early in ontogeny developed into straight, paired spines. American species. ..... Sect. STROMBOCARPA (including "*Sopropis*") (species 5–13).
4. With cauline, axillary, solitary or paired, multi- or uninodal, straight spines. American species.
   a) Spines axillary; shoots differentiated into macroblasts and knotty brachyblasts. Fruit compressed. ..... Sect. ALGAROBIA (syn. *Neltuma*), *pro parte maxima* (species 15–44).
   b) Spines axillary and apical, uninodal, solitary; no brachyblasts. Fruit moniliform. ..... Sect. MONILICARPA (species 14).
5. Secondarily unarmed, because of suppression of the axillary, cauline spines. American species, especially from Paraguay and Argentina. ..... Sect. ALGAROBIA, *pro parte minima* (species 18, 20, 29, 35, 39, etc.).

The term "stipular spines" is ambiguous if not clearly defined. It may mean spinescent stipules, as in sect. STROMBOCARPA, or it may mean geminate, axillary, uninodal, cauline spines developed near the stipules but independent from them, as in sect. ALGAROBIA.

It is interesting to look at another large genus of the Mimosoideae, *Acacia*, to find a similar differentiation. The *Acacia* section or subgenus (Gummiferae Bentham) has spinescent stipules, just as does sect. STROMBOCARPA. *Acacia* subg. ACULEIFERUM Vassal (ser. Vulgares Bentham) has the internodal prickles of *Prosopis* sect. PROSOPIS (although mostly recurved prickles). Then there is one rare *Acacia* species in Australia, *A. pulchella* R. Brown, which has developed primitive, axillary, cauline, uni- or plurinodal, sometimes foliate spines and represents the morphological type of *Prosopis* sect. ALGAROBIA very weakly expressed. The extraordinary leaf polymorphism of the phyllodial acacias in Australia (ser. Phyllodineae Bentham) is not paralleled in *Prosopis*, in which no phyllodes are known. Instead, some species (sect. ALGAROBIA, ser. Sericanthae Burkart) are aphyllous or subaphyllous (leaves small and shed very early in the season), with photosynthesis being accomplished within the cortical tissue of branchlets and spines. This vegetative type is in turn very rare in the genus *Acacia*, although present in a few Australian species.

In other families as well, vegetative differences are also considered to be of infrageneric rank. See, for example, the recent reduction of *Junellia* Moldenke (Verbenaceae) to a section of *Verbena* by N. S. Troncoso (Darwiniana 18: 312. 1974).

There is a floral character which could be considered as important. In sect. ANONYCHIUM, in its only species (and also the only tropical African one), *P. africana* (Guill., Perr., & Rich.) Taubert, the connective of the anther is broadened and the apical gland incurved together with it. This is beautifully portrayed in a recent plate of P. Brenan (in Hubbard & Milne-Redhead, Flora Trop. East Africa 35. London. 1959). At first I thought to use this character as one of sectional value, but later I was able to observe a somewhat similar incurving of the anther gland in *P. farcta* Solander ex Russell) Macbride of sect. PROSOPIS. This fact convinced me again of the generic unity of *Prosopis* in its wider delimitation.

Vegetatively, there is a great diversity in habit. One Oriental species, *P. farcta*, is known by its invading rootsuckers (or rhizomes?), by which it approaches the American *P. strombulifera* (Lam.) Bentham and its relatives. In this and some other characters, sect. STROMBOCARPA comes closer to sect. PROSOPIS than to the entire sect. ALGAROBIA, in which rhizomes or rootsuckers are unknown. However, there remains the basic difference between the two, prickles *versus* spiny stipules.

In sect. PROSOPIS one species, *P. cineraria* (L.) Druce, has longitudinal seeds, another, *P. farcta*, transverse seeds and segments in the fruit. This is a difference to which the rank of series is given in sect. STROMBOCARPA. However, in sect. PROSOPIS the discovery of the new *P. koelziana* Burkart, with its intermediate fruit fabric, reduces the systematic value of this

difference so that no series are distinguished. It is even less possible to revive *Lagonychium* M. Bieb. as a genus for *P. farcta*, as proposed by Bobrov in Komarov's *Flora of the USSR*.

PROBABLE EVOLUTIONARY DEVELOPMENT OF SPECIATION

Prosopis is a rather primitive genus within the Mimosoideae, as the simple pollen grains, the mostly free petals, and the decandrous condition prove. It possibly originated in tropical Africa, where only *P. africana*, the least specialized species, persists. Near relatives are *Adenanthera* L. and *Pseudoprosopis* Harms, with dehiscent legumes. From this or a similar ancestral stock may have evolved the more specialized groups, which have fleshy, indehiscent drupaceous legumes, nearly all with the vegetatively differentiated megablasts and/or brachyblasts (these are absent only in *P. argentina*, aside from in *P. africana*), and with pungent organs (also absent in *P. africana*). The prickly Asian species of sect. PROSOPIS developed in the eastern, arid desert zones. The spiny American ones developed in the western hemisphere into two sharply differentiated, parallel groups, also with desert climate preferences: sect. STROMBOCARPA (with spiny stipules) and sect. ALGAROBIA (with cauline, mostly axillary thorns). In between the two appeared the small section MONILICARPA, with only one isolated member, *P. argentina*, of doubtful origin and affinities. The related genus *Prosopidastrum* Burkart (formerly considered a section of *Prosopis*), with two species, one in Baja California and the other in Patagonia, is a side-branch, which seems to confirm a common origin in one ancient desert floral center. According to the Wegener theory of continental drift, land connections between east and west were easier at the end of the Mesozoic or the beginnings of Tertiary times, when these plant groups must have originated; so the ancestors of present-day *Prosopis* species may have migrated widely from the African center to both east and west, slowly evolving different species that were adapted not to long-distance dispersal, but to a very effective endozoic diffusion through mammals and larger birds (owing to the succulent, edible legumes with hard seeds that escape digestion). Present distribution patterns of species of *Prosopis* do not exclude the possibility of an ancient desert flora common to both Americas which later divided and became widely separated into two centers, the Mexican-Texan center and the Argentine-Paraguayan-Chilean one, where most species occur. The fact that in both centers endemic species exist indicates their antiquity and suggests that long-distance dispersal did play only a secondary role, if any. After millions of years, the speciation process (mainly gene mutations, as suggested by the karyogram uniformity) slowly originated the 40 American species and several varieties now known. Several facts indicate that in America the principal center of origin is Argentina and that the Mexican center is a secondary one. Or perhaps they are of the same age, but some factors, e.g., stronger competition with the boreal floras, prevented a major species development in that northern area of the genus.

TAXONOMIC HISTORY OF THE GENUS

The name *Prosopis*, selected by Linnaeus for this genus, is of ancient Greek origin and means a kind of prickly fruit, such as the head of *Arctium lappa* L. (Compositae). Pfeiffer (Nomencl. Bot. 2(2): 842. 1874) wrote, "Nomen ex Dioscoride, ubi Lappam significat." The interpretation of classic *Prosopis* as a species of *Petasites* (Dictionary of Gardening, Roy. Hort. Soc., Oxford, 1965) is incorrect. Linnaeus, in this case as in others, proceeded arbitrarily, changing a name of age-old tradition and raising the opposition of contemporary, erudite botanists such as Albrecht von Haller. However, at present Linnaeus's name must be accepted. He apparently knew only one species, the type species of *Prosopis* from the Near East, which he called *P. spicigera* in his *Mantissa Plantarum*, published in 1767.

Ludwig Pfeiffer, in his important bibliographic work mentioned above, offers a number of references to the early use of the name since Linnaeus, which I shall not repeat here. However, some of them are of value as milestones in the development of the taxonomy of *Prosopis*.

The *Ceratonia chilensis* of Ignacio Molina (Saggio sulla storia naturale del Chili 172. Bologna. 1782) seems to be the second species described. However, it was ignored for a long time, owing to its inclusion in the wrong genus; its author was misled by the similar Spanish name, structure, and uses of the fleshy legume of the Mediterranean St. John's bread, *Ceratonia siliqua* L. It is *Prosopis chilensis*, the "Algarrobo de Chile" (a big tree of the affinity of *Prosopis juliflora* (Sw.) DC. of northern South America and now the type of ser. Chilenses, ser. nov.) which causes taxonomists so much difficulty.

Mimosa juliflora of Olof Swartz, published in 1788, was the third species recognized, but it was not incorporated into *Prosopis* until 1825. *Mimosa strumbulifera* Lamarck (later corrected to *strombulifera*), Encycl. Méth. Bot. 1: 15, appeared in 1789 and was the first known species of sect. STROMBOCARPA. Willdenow transferred this to *Acacia* (Sp. Pl. ed. 4. 4(2): 1055. 1806).

The voyage of Humboldt and Bonpland to tropical America (1799–1805) contributed various species, first described as species of *Acacia* by Willdenow (*Ibid.* 1058, 1059) and later placed in the proper genus by C. S. Kunth (H.B.K. Nov. Gen. Sp. Pl. folio ed. 6: 305–310. 1823).

The founders of the present limits and subdivisions of the genus are A. P. De Candolle and G. Bentham, the universally known great plant systematists of the 19th century. The former (DC. Prodr. 2: 446 *et passim.* 1825) incorporated the American sect. ALGAROBIA (with the erroneous character "antherae eglandulosae"), enumerating 13 species, if we include the dubious *Prosopis affinis* Sprengel (evidently of this section but listed by De Candolle under species "non satis notae." De Candolle failed to incorporate *Lagonychium* M. Bieb., which is very near sect. ADENOPIS DC., the typical section of *Prosopis*, and he did not recognize sect. STROM-

BOCARPA, defined later by Bentham, in spite of his knowledge of two of its species, *P. torquata* (Lag.) DC. (*loc. cit.* 448) and "*Mimosa*" *strombulifera* Lam. (cited as *Acacia strumbulifera* (Lam.) Willd. in DC. Prodr. 2: 455).

Discrepancies concerning the generic limits of *Prosopis* continued for a time. C. S. Rafinesque Schmaltz, working quite independently and getting no acceptance for his views, founded the genus *Neltuma* Raf. (Sylva Telluriana 119. 1838), with *N. juliflora* as the type. Only a year later, Bentham considered *Prosopis* sect. ALGAROBIA DC. worthy of generic rank (*Algarobia* Bentham, Plantae Hartwegianae 13. 1839), but on false assumptions derived from De Candolle's partially incorrect description. Unfortunately, *Algarobia* is a synonym of *Neltuma* Raf. However, Bentham confirmed De Candolle's diagnosis of the spines, "spec. Americanae spinis nullis aut axillaribus" (Prodr. 2: 446. 1825), of utmost importance in the distinction of sections, stating (*loc. cit.*), "spinae axillares supra stipulas natae ut DC. l. c. in char. sectionis, nec stipulares ut in diagnosibus specificis."

A short time later, Bentham changed his mind and accepted *Prosopis* nearly in its present wider limits (Hooker's Jour. Bot. 4: 346–352. 1842). He maintained his system in the "Revision of the Suborder Mimoseae" (Trans. Linn. Soc. London 30: 376–381. 1875) and was followed by many authors, e.g., P. Taubert (in Engler & Prantl, Nat. Pflanzenfam. 3(3): 118, 119, 385. 1891).

In my paper "Materiales para una monografía del género *Prosopis* (Leguminosae)" (Darwiniana 4: 59, 60. 1940), I accepted and commented upon Bentham's system. In a previous paper on the morphology and ethology of the genus (Darwiniana 3: 24–47. 1937), I tried to give a sound morphological and anatomical basis for the distinction of spines in sects. ALGAROBIA and STROMBOCARPA.

The strongest attack against a wide concept of the genus came in modern times from Britton and Rose in their treatment of "Mimosaceae" (in North American Flora 23(3): 180, 182–187. 1928), followed later by a number of other authors not specialists in the study of Leguminosae. Britton and Rose recognized three genera, *Sopropis*, *Strombocarpa*, and *Neltuma* (*Algarobia*), describing at the same time nine new "species" of *Neltuma*, most of which have since fallen into synonymy. *Sopropis* Britton & Rose (as gen. nov.) is only an outstanding form of *Strombocarpa*. I explain elsewhere in the present paper my opinion that the main differences between sections PROSOPIS, ALGAROBIA, and STROMBOCARPA are the vegetative spine characters and are, therefore, only of subgeneric rank.

Those who prefer to divide the genus (an opinion which I do not sustain) must remember that the section STROMBOCARPA as a genus (*Strombocarpa* Englm. & A. Gray, Boston Jour. Nat. Hist. 5: 243. 1845) is antedated by *Spirolobium* D'Orbigny (Sertum Patagonicum. *tab. 13.* 1839) and sect. ALGAROBIA as a genus (*Algarobia* (DC.) Bentham, Plantae Hartwegianae 13. 1839) by *Neltuma* Raf. (Sylva Telluriana 119. 1838). In this case, *Prosopis* would be reduced to the three Asiatic species

known at present, and all the American ones would become either *Spirolobium* or *Neltuma*. The remaining African section, with only *P. africana*, would also have to be raised to generic rank, because it shows no affinity with the bulk of the American species, nor with the type section of *Prosopis*. This would cause a total change in the nomenclature of many well-known species, with no benefit to anyone. More modern approaches, from the karyological, palynological, and chemotaxonomic researches, do not support (or only slightly support) such a radical subdivision into four genera. Moreover, other large genera of the Mimosoideae, especially *Acacia*, would have to be divided on the same grounds of purely vegetative characters. Finally, why do we have the categories of subgenus, section, and series if we do not use them? These are of great help in expressing intrageneric affinities without the excessive splitting and resulting changes of names so often resisted by those who must use them. I follow here the principles of the *International Code of Botanical Nomenclature*.

Minor changes at the sectional level merit a brief consideration. Bentham, in his famous joint work with Hooker, *Genera Plantarum* (1(2): 591. 1865), defined a section CIRCINARIA with one tropical African species, which he later ("Revision of the suborder Mimoseae," Trans. Linn. Soc. London 30: 515. 1875) reduced to the synonymy of *Acacia albida* Delile. The species was called *P.? kirkii* by Oliver (Fl. Trop. Africa 2: 332. 1871). Such errors concerning the genus are not uncommon in dealing with tropical Mimosoideae when the specimens lack flowers, owing to a certain degree of convergence in the legume characters. Taubert, writing the treatment of the Leguminosae for Engler and Prantl's *Natürlichen Pflanzenfamilien*, accepted sect. CIRCINARIA in the text, but suppressed it in the *errata* section (3(3): 119, 385. 1891).

Another "section" which later had to be suppressed is sect. LOMENTARIA C. Spegazzini (Anal. Soc. Ci. Arg. 47: 286. 1899), based on *Prosopis striata* Bentham, a synonym of *Prosopis globosa* Gillies ex Hooker & Arnott. In a note I tried to clear up the bewildering synonymy of this Patagonian species (Burkart, Physis 20: 53, 54. 1945) without changing its position in sect. LOMENTARIA (Darwiniana 4: 63. 1940). However, the question of the correct genus was raised after the discovery by Dressler of a closely related taxon, *Prosopis globosa* var. *mexicana* Dressler, in Baja California, Mexico. This was later given specific rank, in a new genus, *Prosopidastrum* Burkart (Darwiniana 13: 436–443. 1964), with two species, *P. mexicanum* (Dressler) Burkart (the type) and *P. globosum* (Gillies ex Hooker & Arnott) Burkart. This is a remarkable instance of bicentrism — two very closely related species, one in northwestern Mexico, the other in Patagonia, with no other affinities. The genus *Prosopidastrum* has dehiscent legumes in the type species, but not in the other one; the two species are similar vegetatively, with stipules spiny and recurved and twigs ending in a spine, a combination not found in any *Prosopis*.

A NEW SYNOPSIS OF THE GENUS PROSOPIS
(With Descriptions of the Sections and Series)

Prosopis Linnaeus emend. Burkart.

Type species. *Prosopis spicigera* Linnaeus, Mantissa Pl. 68. 1767; cf. Burkart, Darwiniana 4: 59, 61. 1940. Now a synonym of *P. cineraria* (L.) Druce.

I. **Prosopis** sect. **Prosopis.**

Prosopis sect. *Adenopis* DC. Prodr. 2: 446. 1825.
Lagonychium M. Bieb. Suppl. Fl. Taur. Cauc. 3: 288. 1819.

Shrubs or small trees armed with internodal, straight prickles; no stipular or axillary spines. Flowers in spikelike racemes; petals and ovary entirely glabrous; pollen with areolate exine. Fruit slender or turgid, long or short, very slightly curved; seeds longitudinal or transverse.

Type species. The same as for the genus: *Prosopis cineraria* (L.) Druce.

Distribution. Southwest Asia, North Africa; three species.

II. **Prosopis** sect. **Anonychium** Bentham in Hooker's Jour. Bot. 4: 347. 1842; sect. "*Anonychia*" Bentham, "Revision of the Suborder Mimoseae," Trans. Linn. Soc. London 30: 377. 1875.

Unarmed trees. Leaves well developed; racemes spikelike. Petals glabrous; ovary and style hairy; anther gland introrse, on an expanded, incurved connective; pollen small, the exine perforated, with costae. Legume subterete, straight, thick; seeds longitudinal.

Type species. *Prosopis oblonga* Bentham, *loc. cit.*, a synonym of *P. africana* (Guill., Perr., & Rich.) Taubert.

Distribution. Tropical Africa; only one species.

III. **Prosopis** sect. **Strombocarpa** Bentham in Hooker's Jour. Bot. 4: 351. 1842.

Spirolobium D'Orbigny, Sertum Patagonicum. *tab. 13.* 1839.
Strombocarpa Engelm. & A. Gray, Boston Jour. Nat. Hist. 5: 243. 1845, according to Hutchinson, Gen. Fl. Pl. 1: 287. 1964.

Always spiny shrubs or trees, the spines foliar; stipules lignified, developed into paired, straight, divergent spines of variable length, mostly fused at base and somewhat decurrent from the nodes, external to the

axillary buds or foliate brachyblasts. Flowers in globose to ovoid heads or in more or less elongated spikes; corolla gamopetalous, the petals villous to scarcely pilose within at the tip; pollen medium-sized, the exine thick, ornamented. Leaves with only one pair of pinnae. Fruit straight, curved, or coiled into a dense spiral.

TYPE SPECIES. *Prosopis strombulifera* (Lam.) Bentham.

In this section two series can be distinguished.

Prosopis ser. **Strombocarpae** A. Burkart, ser. nov.

Endocarpii segmenta seminaque longitudinaliter disposita. Legumen rectum, falcatum, vel lateraliter in spiram tortum.

TYPE SPECIES. The same as for the section: *Prosopis strombulifera* (Lam.) Bentham.

DISTRIBUTION. Southwestern United States and Mexico to Chile and Argentina; seven species.

Prosopis ser. **Cavenicarpae** (Burkart) Burkart, comb. nov. BASIONYM: *Prosopis* sect. *Cavenicarpa* Burkart, Darwiniana 4: 76. 1940.

Endocarpii segmenta seminaque in legumine transverse bifariam disposita. Legumen subrectum, falcatum, vel annulare, turgidum, haud lateraliter tortum.

TYPE SPECIES. *Prosopis ferox* Grisebach.

DISTRIBUTION. South America; two species.

IV. Prosopis sect. Monilicarpa Ruiz Leal ex Burkart, sect. nov.

Prosopis sect. *Monilicarpa* Ruiz Leal *nomen nudum* in Cohen, Cei, & Roig, Rev. Fac. Ci. Agr. Univ. Nac. Cuyo 13: 31. 1968.

Frutices ramis teretibus elongatis flexuosis, foliis alternis haud fasciculatis, unijugis; spinae solitariae, axillares, breves, uninodales necnon apicales. Racemi laxi, elongati, pauciflori. Flores pro rata magni, pubescentes; petala intus pilosa; glandula antherali minima. Legumen drupaceum, moniliforme, elongatum, rubrum; articuli ovoideo-globosi haud compressi, isthmi valde constricti; endocarpium osseum.

TYPE SPECIES. *Prosopis argentina* Burkart.

DISTRIBUTION. Western Argentina; one species.

V. **Prosopis** sect. **Algarobia** DC. Prodr. 2: 446. 1825.

Neltuma Raf. Sylva Telluriana 119. 1838.
Algarobia (DC.) Bentham, Plantae Hartwegianae 13. 1839.

Trees, shrubs, or rarely subshrubs without rhizomes, spiny or rarely unarmed; spines cauline, axillary, uninodal, rarely multinodal, solitary or frequently paired and internal in position between the multiple buds and the main internode; stipules small, never spinescent. Flowers in spike-like racemes; petals more or less free, villous inside toward the apex; pollen small, the exine thin, slightly or not at all ornamented. Fruit a drupaceous legume, straight, falcate, annular, or coiled into a very lax and open spiral with 1 to 3 turns, stipitate and acuminate; seeds more or less numerous within, with hard or coriaceous endocarp segments in one longitudinal row.

TYPE SPECIES. *Prosopis juliflora* (Sw.) DC.

DISTRIBUTION. Warmer and drier parts of America; about twenty-nine species.

In this, the largest section, several series can be distinguished.

Prosopis ser. **Sericanthae** Burkart, ser. nov.

Frutices vel arbores subaphyllae, horridae, ramosae; rami spinosi, axillares et terminales, spinas multinodales formantes.

TYPE SPECIES. *Prosopis sericantha* Gillies ex Hooker & Arnott.

DISTRIBUTION. Argentina, Paraguay; two species.

Prosopis ser. **Ruscifoliae** Burkart, ser. nov.

Arbores foliatae; spinae axillares, uninodales, validae, parvae vel nullae, solitariae vel interdum alternatim 1 vel 2. Folia unijuga; foliola saepe pro genere magna vel mediocria, illis serierum sequentium maiores; racemi spiciformes. Legumen elongatum, compressum, articulis subquadratis.

TYPE SPECIES. *Prosopis ruscifolia* Grisebach.

DISTRIBUTION. Gran Chaco (Argentina, Paraguay); four species.

Prosopis ser. **Denudantes** Burkart, ser. nov.

Frutices ramosi, spinosi; spinae axillares, uninodales, semper solitariae. Folia parva vel mediocria, bipinnatim unijuga, caduca. Flores breviter racemosae. Legumen drupaceum, crassiusculum complanatumve, rectum vel incurvatum, subsiccum.

TYPE SPECIES. *Prosopis denudans* Bentham.

DISTRIBUTION. Southwestern Argentina (Patagonia, Cuyo); four species.

Prosopis ser. **Humiles** Burkart, ser. nov.

Frutices vel subfrutices spinosi, ramis (in sicco) striatis. Folia parva, bipinnatim unijuga vel reducta 2-foliolata, caduca. Spinae axillares, geminatae, uninodales, in sicco striatae. Racemi spiciformes, breves. Legumen compressum.

TYPE SPECIES. *Prosopis humilis* Gillies ex Hooker & Arnott.

DISTRIBUTION. Central Argentina, Paraguay; two species.

Prosopis ser. **Pallidae** Burkart, ser. nov.

Arbores vel frutices elati vel nani; spinae uninodales, axillares geminatae. Folia parva vel mediocria, contracta bipinnatim, pauci- vel plurijuga. Racemi elongati, foliis longiores vel subaequales. Legumen compressum, elongatum, subrectum vel annulare; segmenta endocarpi subquadrata vel elliptica, longitudinalia.

TYPE SPECIES. *Prosopis pallida* (Willd.) HBK.

DISTRIBUTION. Argentina to Mexico; seven species.

Prosopis ser. **Chilenses** Burkart, ser. nov.

Arbores vel frutices; spinae uninodales, axillares, geminatae, validae vel parvae, interdum nullae, rarius alternatim 1 vel 2 pro nodo in eodem ramulo. Folia bipinnata pauci-(1–4-)juga, saepe ampla; racemi spiciformes foliis aequilongae vel breviores aut paullo longiores; foliola parva, mediocria usque longiuscule lineares, in rachide approximata vel dissita. Legumen drupaceum elongatum, plus minusve pulposum, lineare, compressum, subrectum, falcatum, annulare vel laxe spiraliter tortum; segmenta endocarpii numerosa, uniseriata, coriacea, saepe subquadrato-ovata, isthmi lati.

TYPE SPECIES. *Prosopis chilensis* (Molina) Stuntz emend. Burkart.

DISTRIBUTION. Southwestern United States and Mexico to Chile, Argentina, and Uruguay; eleven species.

SYSTEMATIC INDEX OF THE KNOWN SPECIES AND VARIETIES OF PROSOPIS

(ARRANGED BY SECTIONS AND SERIES)

Prosopis Linnaeus emend. Burkart

I. *Prosopis* sect. PROSOPIS (syn. sect. *Adenopis*)

1. *P. cineraria*
2. *P. farcta*
   var. *farcta*
   var. *glabra*
3. *P. koelziana*

II. *Prosopis* sect. ANONYCHIUM

4. *P. africana*

III. *Prosopis* sect. STROMBOCARPA (syn. *Spirolobium*)

Ser. Strombocarpae
5. *P. strombulifera*
   var. *strombulifera*
   var. *ruiziana*
6. *P. reptans*
   var. *reptans*
   var. *cinerascens*
7. *P. abbreviata*
8. *P. torquata*
9. *P. pubescens*
10. *P. palmeri*
11. *P. burkartii*

Ser. Cavenicarpae
12. *P. ferox*
13. *P. tamarugo*

IV. *Prosopis* sect. MONILICARPA

14. *P. argentina*

V. *Prosopis* sect. ALGAROBIA (syn. *Neltuma, Algarobia*)

Ser. Sericanthae
15. *P. sericantha*
16. *P. kuntzei*

Ser. Ruscifoliae
17. *P. ruscifolia*
18. *P. fiebrigii*
19. *P. vinalillo*
20. *P. hassleri*
   var. *hassleri*
   var. *nigroides*

Ser. Denudantes
21. *P. denudans*
var. *denudans*
var. *patagonica*
var. *stenocarpa*
22. *P. ruizleali*
23. *P. castellanosii*
24. *P. calingastana*

Ser. Humiles
25. *P. humilis*
26. *P. rojasiana*

Ser. Pallidae
27. *P. rubriflora*
28. *P. campestris*
29. *P. pallida* (including *P. limensis*)
30. *P. affinis* (syn. *P. algarobilla*)
31. *P. articulata*
32. *P. elata*
33. *P. tamaulipana*

Ser. Chilenses
34. *P. chilensis*
var. *chilensis*
var. *riojana*
var. *catamarcana*
35. *P. juliflora*
var. *juliflora*
var. *inermis*
var. *horrida*
36. *P. nigra*
var. *nigra*
var. *ragonesei*
var. *longispina*
37. *P. caldenia*
38. *P. laevigata*
var. *laevigata*
var. *andicola*
39. *P. flexuosa*
forma *subinermis*
40. *P. glandulosa*
var. *glandulosa*
var. *torreyana*
var. *prostrata*
41. *P. alpataco*
42. *P. alba*
var. *alba*
var. *panta*
43. *P. velutina*
44. *P. pugionata*

TENTATIVE KEY TO THE SPECIES OF PROSOPIS THROUGHOUT THE WORLD

1. Petals glabrous. Prickly or unarmed shrubs or trees; no stipular or axillary spines present. Flowers in elongate, spikelike racemes. Legume elongate, slender or thick, straight to subfalcate.
   2. Ovary glabrous. Shrubs or trees mostly armed with internodal, straight, divergent prickles. Stipules caducous, foliaceous, leafletlike or a little larger; leaflets small. Anther gland straight. (Sect. PROSOPIS.)
      3. Leaves 1–3-jugate, glabrous. Legume long-stipitate, the stipe 0.8–2 cm. long; fruit slender, somewhat moniliform, linear to much elongate, cuneate at base. Seed segments longitudinal to transverse.
         4. Legume very slender and elongate, cylindroid-subtorulose, 8–19 cm. long × 4–7 mm. in diameter. Seeds longitudinal, separated from each other, in one row. Spikelike racemes solitary or mostly paniculate; primary bract amplexicaul, with oblique insertion. Southwest Asia. ..... 1. *P. cineraria.*
         4. Legume short-linear, subtorulose, 4–6 cm. long × 8–10 mm. in diameter. Seeds approximated, in transverse-oblique position. Racemes solitary, axillary; bracts lacking. Iran. ..... 3. *P. koelziana.*
      3. Leaves 2–7-jugate, pubescent or glabrous. Legume short-stipitate, turgid, ovoid to thickly terete, rounded and longitudinally furrowed at base, straight or more often inwardly curved. Seeds transverse, in two rows. Racemes solitary, without basal amplexicaul bract. Southwest Asia. ..... 2. *P. farcta.*
   2. Ovary villous or hirtellous. Unarmed trees. Stipules small, not foliaceous; leaflets medium-sized, larger and fewer. Anther gland introrse, on a broad, inwardly curved connective. Legume straight, subterete, thick. (Sect. ANONYCHIUM.) Tropical West Africa to Ethiopia. ..... 4. *P. africana.*
1. Petals internally villous or at least somewhat pilose toward the apex, externally glabrous or pubescent. Ovary pubescent to villous. Trees, shrubs, or subshrubs armed with stipular or axillary spines, sometimes (secondarily) unarmed, never prickly. Flowers in spikelike racemes or heads. Legume elongate, subcylindric or more often compressed, straight, curved, or spirally coiled, rarely moniliform.
   5. Spines foliar; stipules transformed into straight, divergent, paired spines, small or large, but present on all nodes, mostly united at base and more or less decurrent, external in position to the axillary bud or brachyblast (short shoot). Leaves with only one pair of pinnae; leaflets small, numerous. Flowers in spikes or heads, reddish-yellow, corolla gamo- or dialypetalous. Legume straight, falcate, or coiled into an open or dense spiral. Endocarp segments longitudinal or transverse. (Sect. STROMBOCARPA.)
      6. Endocarp segments and seeds in longitudinal position, forming one row; segments developed and closed, or endocarp thin, nearly continuous. Fruits various, ranging from straight to laterally coiled like a corkscrew. Trees or shrubs. (Ser. Strombocarpae.)

7. Legume subterete, nearly straight to subfalcate. Flowers sessile, in spikes. Petals highly connate, nearly glabrous inside. Mexico, Baja California. ..... 10. *P. palmeri.*
7. Legume always laterally curled or coiled in more than 1 or 2 open or closed circles. Flowers in heads or spikes. Petals more or less free.
   8. Flowers in elongate spikes; floriferous rachis 2–8 cm. long.
      9. Legume moniliform, in a few (1–3) coils with a central hole. Endocarp segments bony. Small tree. Central and northwestern Argentina. ..... 8. *P. torquata.*
      9. Legume not or scarcely moniliform, in closed coils without central hole. Endocarp segments coriaceous to thin, delicate, often continuous.
         10. Coils of the legume few (1–3), irregular, submoniliform, several legumes together forming a globose mass. Large, dense shrub with spreading horizontal branches. Northern Chile: Tarapacá. 11. *P. burkartii.*
         10. Coils of the legume numerous, regular, the margins parallel, the spirals usually forming a cylindrical structure. Tree. Southwestern North America. ..... 9. *P. pubescens.*
   8. Flowers in short-cylindric, ovoid or globose heads; floriferous rachis 1 cm. or less long.
      11. Heads ovoid to short-cylindric, 1.5–1.8 cm. long. Legume reddish-brown, in 2 to 7.5 irregular, dense coils. Tall shrub or small tree. Central Argentina. ..... 7. *P. abbreviata.*
      11. Heads perfectly globose. Legume yellow, in more numerous, regular coils. Smaller shrubs forming loose thickets by creeping gemmiparous roots (or rhizomes?).
         12. Leaflets separated, glabrous, in 3 to 8 pairs per pinna. Western Argentina, northern Chile, Peru(?). ..... 5. *P. strombulifera.*
         12. Leaflets close together, mostly pubescent after drying imbricated, in (2 to) 6 to 12 pairs per pinna, smaller. ..... 6. *P. reptans.*
            13. Leaflets pubescent; bracts small. Central Argentina, Peru. ..... 6. *P. reptans* var. *reptans.*
            13. Leaflets glabrous or of a more villous type, especially when young; bracts larger and villous. Texas. ..... 6. *P. reptans* var. *cinerascens.*
6. Endocarp and seeds in transverse position, mostly alternate segments forming two rows. Fruits thicker, subcylindric, nearly straight, falcate or once-annular, ring-shaped, incurved, not laterally coiled. (Ser. Cavenicarpae.)
   14. Tree becoming 15–18 m. tall in age. Stipular spines 0.5–3.8 cm. long. Leaflets obtuse. Legume curved, forming a half to complete ring, subtorulose, 7–11 mm. in diameter, the sutures impressed. Seeds 3–4.3 mm. long. Northern Chile. ..... 13. *P. tamarugo.*
   14. Trees or shrubs 2–5 m. tall. Stipular spines up to 5 cm. long. Leaflets acute or mucronate. Legume straight or

incurved, not torulose, 10–18 mm. in diameter, 2.5–7 cm. long × 1–1.8 cm. thick; placental suture prominent. Seeds 4.5–6 mm. long. Extreme northwestern Argentina, southern Bolivia. ..... 12. *P. ferox.*

5. Spines cauline; thorns resulting from metamorphosed branchlets, multi- or uninodal, long or short, not on all nodes but seldom entirely absent, solitary or frequently in axillary pairs ("geminate"), then internal in position between the multiple buds (brachyblasts or short shoots) and the main branch internode. Leaves with one to 8 pairs of pinnae, sometimes reduced. Racemes spikelike (amentiform), slender; flowers yellowish or sometimes red, the petals little connected, more or less free. Fruit a drupaceous loment, linear, rarely moniliform, straight, falcate or in a few open coils. Endocarp articles longitudinal, in one row. (Sect. MONILICARPA and sect. ALGAROBIA.)
   15. Plants spiny; spines present on at least some nodes, generally better developed on strong shoots than on small twigs.
      16. Spines multinodal; terminal and lateral thorns, with scars representing the reduced leaves. Subaphyllous, horridulous shrubs or trees, with all branchlets spiny. Legume nearly straight or slightly curved, dark or dullish red. (Sect. ALGAROBIA, ser. Sericanthae.)
         17. Shrubs. Calyx and corolla hirtellous outside. Flowering racemes short, ovoid. Spiny twigs slender, ca. 0.8–2.5 mm. in diameter. Legume 7–14 cm. long × 0.8–13 cm. wide, somewhat constricted between the endocarp segments; exocarp dark, dullish red. Northwestern and west-central Argentina. .... 15. *P. sericantha.*
         17. Trees. Calyx and corolla glabrous outside. Flowering racemes slender, elongated. Spiny twigs thicker, ca. 1.2–5 mm. in diameter. Fruit larger, 10–17 cm. long × 1.5–2.6 cm. thick, not constricted, the exocarp nearly black at maturity. Paraguay, southeastern Bolivia, north-central Argentina (Gran Chaco region). ..... 16. *P. kuntzei.*
      16. Spines uninodal; thorns lateral or exceptionally so (*P. argentina*) and some terminal, without scars. Foliage well developed or some species subaphyllous. Fruits varied, yellowish to brown, red, or violet-spotted.
         18. Axillary spines solitary, only one per node, exceptionally solitary or geminate on the same twig. Leaves with one pair of pinnae, rarely bijugate.
            19. Spines axillary and some terminal, small. Branching uniform, with only megablasts (long shoots), but without brachyblasts (short axillary, knotty shoots). Flowers rather large; calyx and corolla pubescent outside. Legume moniliform; segments globose-ovoid, acute, thick, with thin isthmi; exocarp bright red, showy. Anther gland very small. (Sect. MONILICARPA.) Northwest Andean Argentina. ..... 14. *P. argentina.*
            19. Spines always axillary (or lateral). Branching double, with elongate megablasts forming the skeleton of the treetops and abbreviated axillary brachyblasts from multiple buds producing fascicles of smaller leaves and inflorescences. Corolla glabrous or pubescent outside; florets smaller. Legume linear-oblong,

compressed; endocarp segments flat, subquadrate to ellipsoid, with broad, rarely contracted isthmi; exocarp yellow, brown, or violet-spotted. Anther gland larger. (Sect. ALGAROBIA.)

20. Leaflets exceptionally large and broad, 2–10 cm. long × 0.7–3.8 cm. broad, only 2 to 5 pairs per pinna. Spines always solitary, large, up to 33 cm. long. Legume long, compressed, constricted between segments. Trees. (Ser. Ruscifoliae.) ..... 17. *P. ruscifolia.*

20. Leaflets smaller to very small, sometimes medium-sized, or if long, then linear, narrow.

21. Spines always solitary per axil. Leaflets small, 1.5–12 mm., exceptionally to 15 mm. long, alternate on lower part of pinna. Leaves small to medium-sized (*P. ruizleali*). Shrubs. Racemes medium to short. (Ser. Denudantes.) Argentine endemics: Cuyo and Patagonian provinces.

22. Racemes spikelike; flowers pedicellate. Leaflets distant on the rachis.

23. Twigs without prominent nerves, soon reddish-brown. Legume turgid, nearly black at maturity, glabrous. Leaves glabrous.

24. Leaves small, with 1 to 4 pairs of leaflets per pinna. Legume falcate to annular, sometimes straight or thin. Argentina: Patagonia. ..... 21. *P. denudans.*

24. Leaves larger, to 8–9 cm. long, with 3 to 9 pairs of leaflets per pinna. Legume thick, straight, falcate to subannular. Western Argentina: Mendoza and Neuquén. ..... 22. *P. ruizleali.*

23. Twigs longitudinally nerved, green for a longer period. Legume compressed, olive-brown, pubescent. Leaflets pubescent, 4 to 7 pairs per pinna. West-central Argentina: Prov. San Juan. ..... 24. *P. calingastana.*

22. Short, subglobose flower heads; florets sessile. Leaflets very small, approximate-imbricate, 1.6–3.5 mm. long, 3 to 12 pairs per pinna. Twigs greenish, with several longitudinal, prominent nerves. Legume broadly oblong, much flattened, somewhat curved; pericarp thin, dry; segments subquadrate. Western Argentina: Mendoza and Neuquén. ..... 23. *P. castellanosii.*

21. Spines solitary or geminate alternately along the branchlets, sometimes all solitary. Leaflets larger, medium-sized to long and narrow, mostly 15–63 mm. long, exceptionally only 8 mm. long, opposite on the pinnae. Leaves medium to rather large. Spikelike racemes cylindrical, long. Trees or large shrubs.

25. Legume not moniliform, its margins parallel or subparallel. Spines short.

26. Leaflets oblong, less than 5 times as long as broad, herbaceous, ca. 6–23 mm. long ×

1.6–5.5 mm. broad. Legume straight, falcate only at the apex, mostly straw-colored or brown. Trees or tall shrubs. Tropical coasts, Mexico, Central America, Antilles, northern South America. Also cultivated. (Ser. Chilenses.) ..... 35. *P. juliflora* var. *juliflora.*

26. Leaflets linear (except for abnormal, diseased(?) ones usual on the same twigs), more than 5 times longer than broad, subcoriaceous, ca. 0.7–63 mm. long × 1.5–4.5 mm. broad. Legume straight, brownish. Trees or shrubs, erect to prostrate. Southwestern North America. ..... 40. *P. glandulosa.*

25. Legume moniliform, slender, elongate, compressed, its margins undulate, faces spotted. Spines large, small, or absent. Leaflets tending to fusiform, 10–30 mm. long × 2–12 mm. broad. Argentina: Gran Chaco. (Ser. Ruscifoliae.) ..... 19. *P. vinalillo.**

18. Axillary spines geminate, nearly constantly two pairs of spines per node. Leaves with 1 to 8 pairs of pinnae, in most species ample, 1–3-jugate, in some reduced.

27. Leaves reduced, very small, deciduous, dominated by the well-developed, long spines. Subaphyllous glabrous shrubs or subshrubs. Twigs and spines longitudinally striate. Legume subfalcate, compressed. (Ser. Humiles.)

28. Subshrub with woody rootstocks; branchlets and spines prominently nerved and sulcate. Flowers bright red. Leaves 1-jugate, the leaflets 1 to 3 pairs per pinna, small, oval; or leaves simply pinnate, with 1 to 2 pairs of leaflets. Spikes frequently replacing one spine of a pair. Central Argentina. ..... 25. *P. humilis.*

28. Larger shrub or tree; branchlets and spines longer, less striate. Flowers dull in color. Leaves always bipinnate, 1-jugate; petiole dilated at summit; leaflets 8 to 17 pairs, small, imbricate. Paraguay: Chaco. ..... 26. *P. rojasiana.*

27. Leaves well developed or if small, never simply pinnate. Twigs and spines terete, neither nerved nor sulcate.

29. Pinnae 3 to 8, mostly 5 pairs per leaf. Stamens and styles bright red. Racemes long, slender, longer than the leaves; leaflets numerous, small, approximate. Medium-sized tree; spines small. Northeastern Paraguay. (Ser. Pallidae.) ..... 27. *P. rubriflora.*

29. Pinnae only 1 to 4 pairs per leaf. Flowers greenish-white to yellowish with age.

* See also species no. 20, *P. hassleri*, with small spines.

30. Dwarf, 10–50 cm. tall, prostrate, extended, much-branched, hard, thorny little shrub. Leaves small, with 1 to 2 pairs of pinnae, pubescent; leaflets 1.5–6 mm. long, linear, approximate, 6 to 17 pairs per pinna. Racemes ovoid-cylindric; flowers pubescent. (Ser. Pallidae.) Central Argentina: Córdoba mountains. ..... 28. *P. campestris.*

30. Larger shrubs or trees, mostly 1 m. to more than 15 m. tall. Pinnae 1 to 4 pairs.

31. Leaves small, contracted; racemes long, slender, longer than or equalling the leaves. Leaflets approximate, pubescent to glabrous or only ciliolate. (Ser. Pallidae and ser. Chilenses *pro parte.*)

32. Legume dry, compressed, its margins undulate, the pericarp thin; endocarp segments rhombic, with longitudinal or oblique seeds, the isthmi very narrow, central. Leaves 1(–2)-jugate; leaflets 6 to 20 pairs per pinna; pinnae 0.4–6.5 cm., shorter than or equalling the racemes. Northwestern Mexico. ..... 31. *P. articulata.*

32. Legume fleshy, compressed but thicker; endocarp segments ovate to subquadrate, the isthmi broad, nearly as broad as the segments. Leaves various.

33. Leaflets prominently pinnatinerved below; 6 to 30 pairs per pinna, broadly oblong, obtuse, 2–8.3 mm. long, more or less pubescent or ciliate. Legumes straight with parallel margins or little constricted.

34. Legumes broad, 0.9–1.6 cm. in diameter.

35. Leaflets obtuse or obtuse and mucronate, 6 to 15 pairs per pinna, 2.5–8.3 mm. long and 1.4–4 mm. broad. Spines small, sometimes absent. Legume straight, thick, straw-yellow, 1–1.5 cm. broad, glabrous. Southern Colombia to Peru; Hawaiian Islands. ..... 29. *P. pallida.*

35. Leaflets subacute or acute, 10 to 30 pairs per pinna, linear, 2–7.5 mm. long × 0.8–1.8 mm. broad. Spines small. Legume submoniliform, annular, spotted, glabrous, 0.9–1.6 cm. broad. Northeastern Argentina, Paraguay. ..... 30. *P. affinis.*

34. Legumes narrow, 0.6–0.8 cm. broad.

36. Spines strong, divergent horizontally, the internodes to 7.5 cm. long, often constricted at base. Foliage green. Legume straight, pubescent. Tall shrubby tree. Western Gran Chaco. ..... 32. *P. elata.*

36. Spines weak, never horizontally divergent. Foliage small, glaucous.

Legumes straight, glabrous or puberulous. Small trees. Mexico: Tamaulipas. ..... 33. *P. tamaulipana.*

33. Leaflets without nerves or only the midrib (costa) visible below. Leaves small, delicate; racemes longer. Large tree. Central Argentina. ..... 37. *P. caldenia.*

31. Leaves larger, ample, expanded, lax, equalling the racemes in length or a little longer or shorter. Leaflets numerous, distant or approximate on the rachis. Trees or shrubs.

37. Leaflets small, 2–7.5(–10) mm. long, linear-oblong, obtuse, approximate, overlapping, touching each other or separated by less than their own width; glabrous or rarely ciliolate. Trees or large shrubs. (Ser. Nigrae.)

38. Trees, becoming large in age, the tops round with pendulous twigs and neat trunk. Spines small, absent on small branchlets.

39. Leaflets pubescent, close together on the pinna. Mexico. .. 43. *P. velutina.*

39. Leaflets glabrous.

40. Leaflets oblong, reticulately pinnate-nerved below, 4–7 mm. long × 1.2 mm. broad, neither distant nor approximate, touching the rachis. Legume straight to subfalcate, compressed-moniliform. Central Argentina and the Gran Chaco. ..... 36. *P. nigra.*

40. Leaflets linear, smaller, without nerves or only the midrib (costa) visible below, 2.7–5.4 mm. long × 0.2–1.1 mm. broad, approximate. Legume falcate to coiled in 2 to 3 open, lax spirals, not moniliform. South-central Argentina. ..... 37. *P. caldenia.*

38. Large shrub. Spines large, directed horizontally, stout. Argentina: western Gran Chaco (see ser. Pallidae in key (31) above). ..... 32. *P. elata.*
With slender, long spines; trees. ..... 36. *P. nigra* var. *longispina.*

37. Leaflets (or at least most of them) larger, 4–63 mm. long. (Ser. Chilenses and a transitional species of ser. Ruscifoliae.)

41. Leaflets pubescent, medium-sized, 5–15(–20) mm. long × 2–4.8 mm. broad. Pinnae 1 to 4 pairs.

42. Legume glabrous. Leaflets distant, 12 to 14 pairs per pinna, pubescent to subglabrous. Racemes 9–12 cm. long. Twigs soon blackish or gray. Northern Peru. ..... 35. *P. juliflora* var. *horrida.*

42. Legume velvety pubescent, mainly when unripe. Leaflets approximate, 12 to 30 pairs per pinna, pubescent. Racemes 5–10 cm. long. Twigs greenish-brown. Southwestern North America. ..... 43. *P. velutina*.

41. Leaflets glabrous or only ciliolate on the margins, medium-sized to large.
    43. Leaflets large, 10–63 mm. long, glabrous, separated on the rachis by more than their own width.
        44. Leaflets linear, narrow, or in some varieties broader, 1.1–5.4 cm. long × 1.1–3(–5) mm. broad; costa visible but of the same color as the mesophyll; secondary veins absent, obscure, or a few subparallel from base. Legume broad to narrow, straight, falcate, or annular according to varieties. Large trees or tall shrubs; spines always geminate, sometimes absent. Peru, Bolivia, central Chile, northwestern Argentina. ..... 34. *P. chilensis*.
        44. Leaflets somewhat broader or veins more visible; costa light-colored, contrasting with the mesophyll. Spines alternately geminate or solitary on the same shoot. Legumes straight.
            45. Leaflets lanceolate to elliptic-oblong or fusiform, 10–30 mm. long × 2–12 mm. broad. Legume slender, elongate, subfalcate or straight, compressed-moniliform. Tree. Argentina: Gran Chaco. ..... 19. *P. vinalillo*.
            45. Leaflets linear to oblong-linear, 7–63 mm. long, distant, 5 to 15 times as long as broad. Usually shrubby. Legume thicker. North America: Texas, Mexico. ..... 40. *P. glandulosa*.
    43. Leaflets medium-sized, ca. 4–23 mm. long, approximate or distant, glabrous or only ciliolate on margins.
        46. Leaflets elliptic-oblong, broad, usually not separated by more than their own width.
            47. Leaflets ca. 15 to 41 pairs per pinna, approximate, subcoriaceous, 5–15 mm. long, 2 to 7 times as long as broad. Legume straight, thick. Mexico. ..... 38. *P. laevigata*.
            47. Leaflets less than 30 pairs per pinna, more distant.

48. Leaflets herbaceous, oblong, pinnatinerved, corrugated when dry, 6 to 15 pairs per pinna, 10–23 mm. long. Trees or tall shrubs; spines rather small, geminate or alternately solitary and paired. Legume elongate, subfalcate, yellow, with parallel margins. Tropical coasts, Antilles, northern South America, and Central America. ..... 35. *P. juliflora.*

48. Leaflets subcoriaceous, thicker, not becoming corrugated by dessication, distant on the rachis.

49. Leaflets short, 4–12 mm. long. West-central Argentina. ..... 39. *P. flexuosa.*

49. Leaflets longer, 15–25 mm. Mexico, southwestern United States. ..... 40. *P. glandulosa* var. *torreyana.*

46. Leaflets very narrowly linear.

50. Large trees. Leaflets numerous, 25–50 pairs per pinna, moderately separated or approximate, 5–17 mm. long × 1–2 mm. broad. Legume much compressed, yellow, falcate to annular; margins parallel; pulp sweet. Central and northwestern Argentina. .. 42. *P. alba.*

50. Trees or shrubs. Leaflets less numerous and the pairs farther apart on the rachis; distance greater than the width of the leaflets.

51. Tall (0.2–3 m.) shrub with thick underground horizontal branches and thin erect aerial shoots. Pinnae 1 to 2 pairs, 3–14 cm. long; leaflets 9 to 25 pairs, 5–17(–30) mm. long × 0.9–1.5 mm. broad. West-central Argentina. ..... 41. *P. alpataco.*

51. Trees or tall shrubs with trunk, this sometimes short.

52. Spines very long and strong. West-central Argentina. ..... 44. *P. pugionata.*

52. Spines small or scarce. Western Argentina. ..... 39. *P. flexuosa.*

15. Plants unarmed; spines probably absent by reduction. Trees. (Various series of sect. ALGAROBIA.)

53. Leaflets large, 0.8–6.5 cm. long. Branchlets reddish; leaves darkening when dry, 1-jugate.

54. Leaflets large, 2 to 9 pairs per pinna, 2.5–6.5 cm. long × 2–4 cm. broad, similar to those of *P. ruscifolia*, but more nearly ovate, obtuse, darkening when dry. Legume linear, compressed, yellow, its margins parallel. Paraguay; Argentina: Formosa (eastern Chaco). ..... 18. *P. fiebrigii.*
54. Leaflets somewhat smaller, more nearly linear and more numerous, 6–26 pairs per pinna, 0.8–4 cm. long × 1.8–16 mm. broad, glaucous-reddish when dry. Legume similar. Paraguay; Argentina: eastern Formosa to northern Santa Fe. ..... 20. *P. hassleri.*

53. Leaflets much smaller, ovate or linear. Branchlets not reddish.
55. Leaflets glabrous. Leaves 1–2-jugate.
56. Leaflets distant, 5–13 mm. long. Heartwood dark. Western Argentina. .. 39. *P. flexuosa* var. *subinermis.*
56. Leaflets approximate, shorter, 1.5–3.2 mm. long. Heartwood yellow. Argentina: Santa Fe. ..... 36. *P. nigra* var. *ragonesei.*
55. Leaflets pubescent.
57. Racemes longer than the leaves. Leaflets 2.5–8.3 mm. long. Southern Colombia, Ecuador, northern Peru, Hawaiian Islands. ..... 29. *P. pallida* forma *pallida.*
57. Racemes of nearly the same length as the leaves. Leaflets 6–20 mm. long. .. 35. *P. juliflora* var. *inermis.*

TABLE 1. The natural geographic areas of development of species of Prosopis.

AREA	TOTAL NO. OF SPECIES	SPECIES
SOUTHWEST ASIA AND NORTH AFRICA	3	*P. cineraria*; *P. farcta*; *P. koelziana.*
TROPICAL AFRICA	1	*P. africana.*
TEXAN-MEXICAN AREA	8	*P. pubescens*; *P. palmeri*; *P. articulata*; *P. tamaulipana*; *P. juliflora*; *P. laevigata*; *P. glandulosa*; *P. velutina.*
TROPICAL ANDEAN REGION (Colombia to the extreme north of Chile and northwest of Argentina)	6	*P. burkartii*; *P. ferox*; *P. tamarugo*; *P. pallida* (including *P. limensis*); *P. chilensis*; *P. juliflora.*
ARGENTINIAN-PARAGUAYAN CENTER AND NEIGHBORING AREAS		
GRAN CHACO AND ADJOINING AREAS	23	*P. strombulifera*; *P. reptans*; *P. abbreviata*; *P. torquata*; *P. sericantha*; *P. kuntzei*; *P. ruscifolia*; *P. fiebrigii*; *P. vinalillo*; *P. hassleri*; *P. humilis*; *P. rojasiana*; *P. rubriflora*; *P. campestris*; *P. affinis*; *P. elata*; *P. chilensis*; *P. nigra*; *P. caldenia*; *P. flexuosa*; *P. alpataco*; *P. alba*; *P. pugionata.*
PATAGONIAN AND CUYO REGION	5	*P. argentina*; *P. denudans*; *P. ruizleali*; *P. castellanosii*; *P. calingastana.*

THE NATIVE AND INTRODUCED SPECIES OF PROSOPIS A GEOGRAPHICAL ENUMERATION

Numbers in parentheses represent the number of the species in the text.

ASIA AND NORTH AFRICA

NATIVE SPECIES

P. cineraria (1): Arabia; Iran, Afghanistan, Pakistan, and India.

P. farcta vars. **farcta** and **glabra** (2): Algeria and Tunisia; Egypt; Turkey and Cyprus; Syria and Israel; Iraq, Iran, Afghanistan, and Pakistan; USSR: Transcaucasia and Turkestan.

P. koelziana (3): Iran.

INTRODUCED SPECIES

P. pallida (29): India.

P. juliflora (35): Iraq, Pakistan, India, and Vietnam.

P. glandulosa (40): Southern Arabia, Pakistan, India, and Burma.

NOTES. Species successfully grown in the botanical garden at El Staff in middle Egypt: **P. alba, P. nigra, P. laevigata** (? sub **P. chilensis** and **P. dulcis**), **P. glandulosa, P. affinis** (sub **P. nandubay**), **P. kuntzei** (sub **P. kunzii**), **P. pubescens, P. strombulifera,** and the Oriental **P. cineraria** (sub **P. spicigera**); see Warda H. Bircher, *Gardens of the Hesperides*, 343–347. 1960.

TROPICAL AFRICA: one native species.

P. africana (4): Senegal, Guinea-Bissau to Nigeria, Cameroons, Sudan, Uganda, and Ethiopia.

SPECIES IN CULTIVATION
P. juliflora var. **juliflora** (35): Senegal.

SOUTH AND SOUTHWEST AFRICA: introduced species only.

P. pubescens (9).
P. chilensis var. **catamarcana** (34).
P. glandulosa (40).

PACIFIC ISLANDS (Hawaii, Marquesas, and the Philippines): introduced species only.

P. pallida formae **pallida** and **armata** (29).
P. juliflora (35).

AUSTRALIA: introduced species only.

P. pallida (29): only in cultivation.
P. chilensis? (34).
P. juliflora (35): Queensland.
P. glandulosa (40).
P. velutina (43): cultivated.

AMERICA: native species only.

UNITED STATES (continental): 5–7 species; none endemic.

P. strombulifera? (5): California.
P. reptans var. **cinerascens** (6): Texas, Oklahoma, and southeastern Colorado.
P. pubescens (9): Texas to southern California and southern Utah.
P. articulata (31): Arizona.
P. laevigata (38): Texas, rare.
P. glandulosa vars. **glandulosa, prostrata,** and **torreyana** (40): California to Kansas, Texas, and Louisiana.
P. velutina (43): Southern Arizona, California.

MEXICO: 9 native species; 3 endemic.

P. reptans var. **cinerascens** (6).
P. pubescens (9).
P. palmeri (10).
P. articulata (31).

P. tamaulipana (33).
P. juliflora (35).
P. laevigata (38).
P. glandulosa vars. **glandulosa, torreyana,** and **prostrata** (40).
P. velutina (43).

CENTRAL AMERICA (Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama).

P. juliflora (35).

ANTILLES (West Indian Islands: Cuba, Hispaniola, Jamaica, Puerto Rico, and many smaller islands): probably only species introduced from the mainland.

P. pallida (29): including **P. limensis.**
P. juliflora (35).
P. glandulosa (40): cultivated in Puerto Rico; see León & Alain, Fl. Cuba 2: 251. *fig. 108.* 1951.

VENEZUELA

P. juliflora (35).

COLOMBIA

P. pallida (29).
P. juliflora (35).

ECUADOR

P. pallida (29).
P. juliflora vars. **juliflora** and **inermis** (35).

PERU: 5–6 species, all native; none endemic.

P. strombulifera? (5).
P. reptans (6).
P. pallida (29): including **P. limensis.**
P. chilensis (34).
P. juliflora vars. **juliflora, horrida,** and **inermis** (35).
P. laevigata var. **andicola** (38).
P. alba var. **panta** (42).

BOLIVIA: 7–8 native species; none endemic.

P. ferox (12).
P. kuntzei (16).
P. ruscifolia (17).
? **P. affinis** (30).
P. chilensis (34).
P. nigra (36).
P. laevigata var. **andicola** (38).
P. alba var. **panta** (42).

CHILE: 6 native species; 2 endemic.

P. strombulifera (5).
P. burkartii (11).
P. tamarugo (13).
P. chilensis var. **chilensis** (34).
P. flexuosa (39): including **P. fruticosa.**
P. alba var. **panta** (42).

PARAGUAY: 11 native species; 2 endemic.

P. kuntzei (16).
P. ruscifolia (17).
P. fiebrigii (18).
P. vinalillo (19).
P. hassleri (20).
P. rojasiana (26).
P. rubriflora (27).
P. affinis (30).
P. elata (32).
P. nigra (36).
P. alba var. **panta** (42).

BRAZIL: 3 native species on very small areas, 1 introduced; none endemic.

P. ruscifolia (17): Piauhy/Parahyba (very local, introduced?).
P. rubriflora (27): extreme south of Mato Grosso.
P. affinis (30): extreme southwestern Rio Grande do Sul.
P. juliflora (35): *sensu stricto*, *haud sensu* Bentham in Fl. Brasil., 1876; introduced, cultivated, northern states.

URUGUAY: 3 native species.

P. affinis (30).
P. nigra (36).
P. alba (42).

ARGENTINA: native species only, ca. 28; 13 endemic. Center of polymorphism of the genus.

P. strombulifera vars. **strombulifera** and **ruiziana** (5).
P. reptans var. **reptans** (6).
P. abbreviata (7).
P. torquata (8).
P. ferox (12).
P. argentina (14).
P. sericantha (15).
P. kuntzei (16).
P. ruscifolia (17).
P. fiebrigii (18).
P. vinalillo vars. **vinalillo** and **parvifolia** (19).
P. hassleri vars. **hassleri** and **nigroides** (20).
P. denudans vars. **denudans, patagonica,** and **stenocarpa** (21).

P. ruizleali (*22*).
P. castellanosii (*23*).
P. calingastana (*24*).
P. humilis (*25*).
P. campestris (*28*).
P. affinis (*30*).
P. elata (*32*).
P. chilensis vars. **chilensis, riojana,** and **catamarcana** (*34*).
P. nigra vars. **nigra, ragonesei,** and **longispina** (*36*).
P. caldenia (*37*).
P. laevigata var. **andicola** (*38*).
P. flexuosa formae **flexuosa** and **subinermis** (*39*).
P. alpataco (*41*).
P. alba vars. **alba** and **panta** (*42*).
P. pugionata (*44*).

(To be concluded)